THE SPATANGOID ECHINOID *LOVENIA* FROM THE TERTIARY OF SOUTHEASTERN AUSTRALIA

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A study of three localities in the Tertiary of southeastern Australia revealed that the spatangoid echinoid *Lovenia* Desor is represented by the species *L. forbesii* (Woods, 1862), *L. woodsii* (Etheridge, 1875) and *L. bagheerae* sp. nov. A preliminary qualitative study of the three species demonstrated the changes that occur during ontogeny.

TERTIARY marine strata are developed widely in southeastern Australia in major basins including the Murray, Otway, Bass and Gippsland basins (Fig. 1). Reviews of the stratigraphy of these deposits were provided by Singleton (1968), Darragh (1985), Mallett & Holdgate (1985) and Abele et al. (1988). These reviews also provide details of the local southeastern Australian stage terminology and the correlation of stratigraphical sections and stages with Australian and international planktic foraminiferal zones. Truswell et al. (1991) provide the most recent survey of international correlations for the Australian Tertiary successions.

Details of stratigraphical units (formations), localities and ages of the strata yielding the collections for the present study are provided with the descriptions of the species; general localities are shown on Fig. 1.

Usage of specific names. There has been considerable confusion regarding authorship of *Spatangus forbesii*. The specific name was originally attributed by Woods (1859) to specimens from Portland and Mt Gambier and later applied by Woods (1860, 1862) to specimens reputed to be from Mt Gambier. Of the illustrated account (1862: 75, 83), the second figure, is a reproduction of Sturt's (1833: pl. 3)

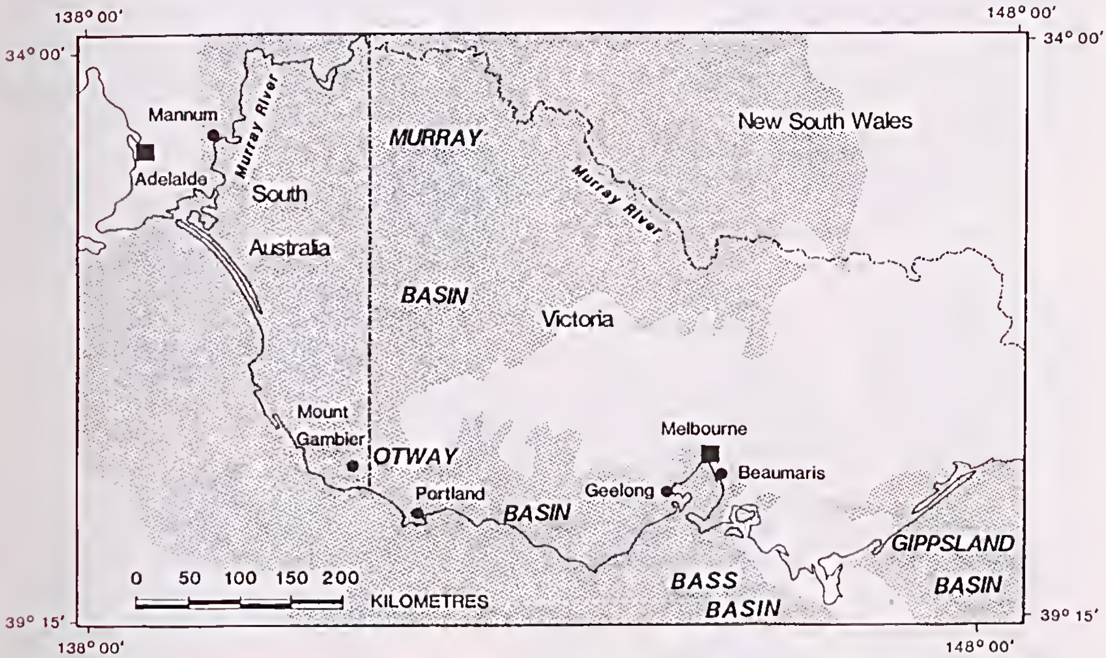


Fig. 1. Distribution of Tertiary marine strata in southeastern Australia and general localities mentioned in text.

Murray River cliffs specimen. Despite the absence of a formal diagnosis, Woods' illustrated account (1862) appears to satisfy the provisions of the International Code of Zoological Nomenclature for the validity of the specific name and authorship. Subsequently, Etheridge (1875) recognised *L. woodsii* from Beaumaris. This species was invariably synonymized by later workers with *L. forbesii*, and it was not until midway through the twentieth century (Pritchard 1976; paper actually written in 1947) that *L. woodsii* was again recognized as a distinct species. Nevertheless confusion over the use of specific names has persisted.

The Portland population of *Lovenia* investigated for this study has previously been assigned to both *L. woodsii* (e.g. Carter 1963; Singleton 1968; Abele et al. 1988) and *L. forbesii* (Murray 1985) without critical investigation but is shown by us to represent a distinctive new species.

SYSTEMATIC PALAEONTOLOGY

Terminology used in the descriptions below is that of Melville & Durham (1966).

All material is housed in the Department of Invertebrate Palaeontology, Museum of Victoria.

Class ECHINOIDEA Leske, 1778

Order SPATANGOIDA Claus, 1876

Family LOVENIIDAE Lambert, 1905

Genus **Lovenia** Desor, 1847

Type species. *Spatangus elongatus* Gray, 1845.

Diagnosis. See Fischer (1966).

Lovenia forbesii (Woods, 1862)

Fig. 2

Spatangus Hoffmanni, Goldfuss.—Sturt 1833: 254, pl. 3, fig. 10.
Spatangus Forbesii Woods 1862: 83.
Spatangus Forbesi, Woods.—Duncan 1864: 165, ? pl. 6, fig. 3.
Hemipatagus Forbesi, Woods & Duncan.—Duncan 1864: 165, ? pl. 6, figs 3-? Woods 1867b: 1–2, fig. 3.
Hemipatagus Forbesii, Woods & Duncan.—Woods 1867a: 1.—Duncan 1870: 285.
Hemipatagus Forbesi, Woods sp.—Laube 1869: 193–194, fig. 4.
Lovenia Forbesi, Woods & Duncan.—Duncan 1877: 44, 56–61, pls 4/5–8.
Lovenia Forbesi var. *Woodsi*, Etheridge.—Duncan 1877: 44, 56–61, 63, pl. 4, figs 5–8.
Lovenia Forbesii, Woods & Duncan.—Etheridge 1878: 141.—Woods 1878: 76.
Lovenia Forbesii, var. *Woodsii*, Etheridge.—Etheridge 1878: 141.
Lovenia Forbesi, McCoy.—McCoy 1879: 37–40, pl. 60, figs 1–4.
Lovenia Forbesii, Woods.—Tate 1885: 37, 39, 41.
Lovenia Forbesi.—Tate 1885: 34.
Lovenia Forbesi, var. *Woodsii*, Etheridge.—Johnston 1887: 130.
Lovenia Forbesi, Duncan.—Pritchard 1892: 186.
Lovenia Forbesi, Woods.—Tate & Dennant 1893: 226.
Lovenia forbesi.—Brown 1910: 4.—Ludbrook 1957: 178.—Ludbrook 1958: 108–110.—Ludbrook 1961: 38, 43, table 1.—Ludbrook 1969: 180.—McNamara 1991b: 42, figured, 43, figured, 44.
Lovenia forbesi, Woods.—Chapman 1914: 147, 150.—Chapman 1915: 44.—Howchin 1928: 402–403, fig. 172/c.—Ludbrook 1961: 44, 45, 48, 60, 62, pl. 8, figs 5, 6, table 1.—Sadler, Pledge & Morris 1983: 25.—McNamara & Ah Yee 1989: 177.
Lovenia forbesii, Woods.—Philip 1963: 184.—Archbold 1990: 119, figs A, C.
Lovenia forbesi, Woods & Duncan.—Aslin 1980: 9, figs 5–8.—Holmes 1987: 33, fig. 4.
Lovenia forbesii.—Abele 1988: pl. 4-1/b, c.
Lovenia.—Brown & Stephenson 1991: 429.

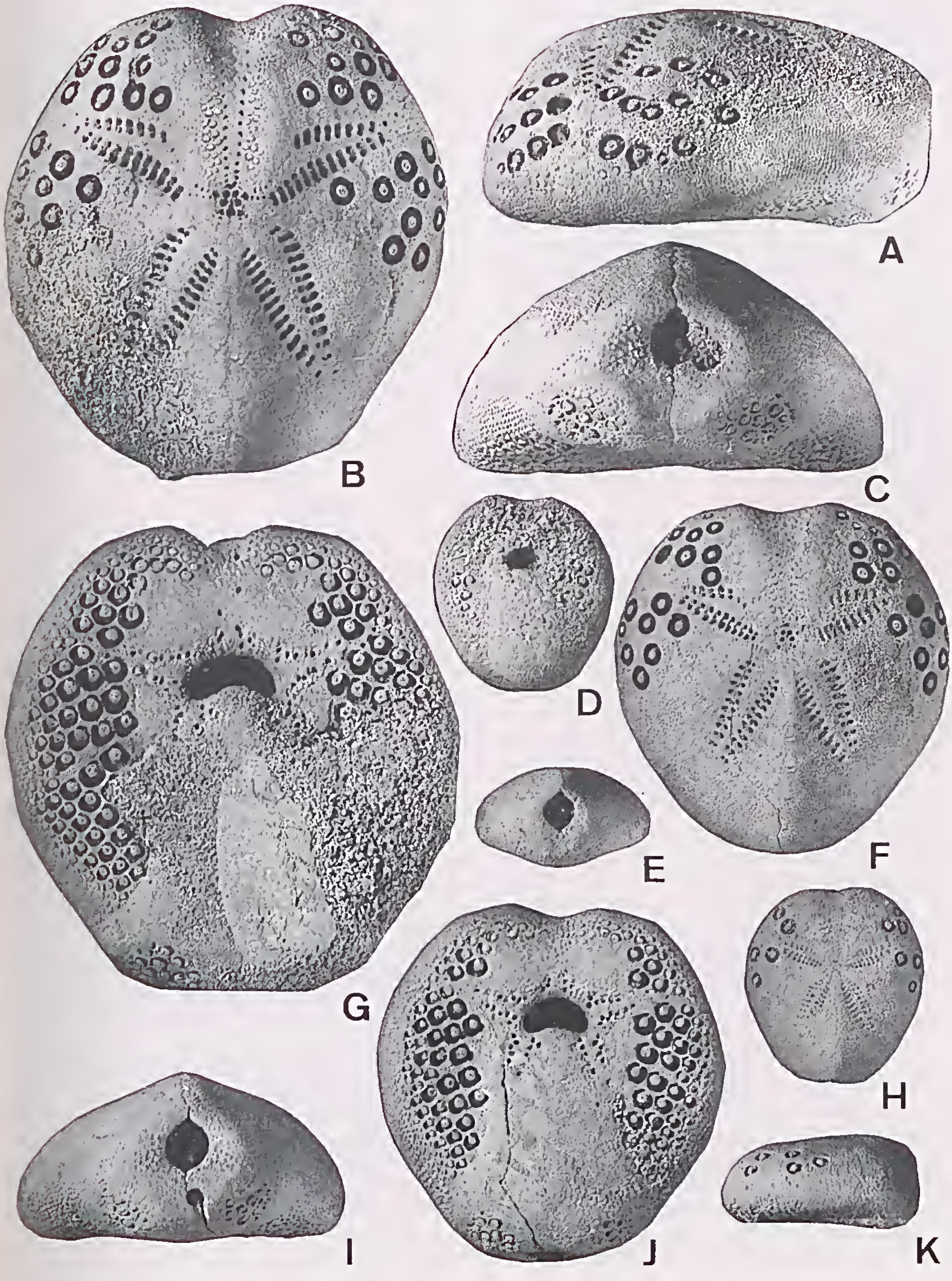
Lectotype. The location of both Sturt's and Wood's original specimens are unknown therefore in the interests of nomenclatural stability, the specimen figured by Sturt, pl. 3, fig. 10, and redrawn by Woods, p. 83, is herein selected as lectotype according to ICZN 3rd edn. Article 74(c). The specimen is from the fossiliferous Murray River cliffs of South Australia, believed to be the Early Miocene (Longfordian) Mannum Formation.

Material and locality. NMV P78919–P78957, 34 specimens from the Longfordian (Aquitanian–Burdigalian) Mannum Formation, Murray Basin with the general location Murray cliffs were examined, excluding NMV P78927, P78935, P78941, P78943, P78951 which are from the Port Campbell Limestone at Portland and are here assigned to *L. bagheerae* sp. nov.).

Size ranges. Length 14.2–36.6 mm; width 12.9–34.4 mm; height 6.9–19.6 mm; width as % of test length 87–96%; (mean 91%); height as % of test length 45–56%; (mean 50%).

Diagnosis. Test distinctly heart-shaped with maximum width less than half-way from anterior end. Shallow anterior sulcus. Large number of primary tubercles, extending into posterior half of test;

Fig. 2. A–K, *Lovenia forbesii* Woods. All figures ×2. A, C, NMV P78929, lateral and posterior views; B, G, NMV P78946, adapical and adoral views; D, E, H, K, NMV P78919, adoral, posterior, adapical and lateral views; F, I, J, NMV P78937, adapical, posterior and adoral views.



frequently in interambulacra 2a/3b. Antero-lateral petals terminate half way to ambitus, equal in width and length to posterior petals, ambulacra IIb/IVa ½–⅓ length of IIa/IVb. Periproct elongated in dorso-ventral plane, peristome antero-posteriorly broad.

Remarks. Both Duncan (1877) and McCoy (1879) included a combination of characters now known to embrace both *L. forbesii* and *L. woodsii*. McCoy (1879) recognised that the Murray cliffs specimens differed from those near Melbourne by possessing a greater number of tubercles, a less pentagonal test and a more anteriorly positioned apex. Nevertheless, he and Duncan (1877) considered *L. forbesii* to be highly variable. McCoy also considered that *L. forbesi* var. *minor* (Duncan 1877) exceeded the difference in variation, and so lacked validity.

Forbes (1852) reported on echinoids from the Murray River and *Spatangus* from Melbourne. His figure b, on page 50 is labelled *Spatangus*, implying Melbourne as the locality, yet the test outline and large peristome resembles *L. forbesii*. Duncan (1864) described *L. forbesii* from the Murray River cliffs and Mount Gambier, the figure resembling *L. bagheerae* sp. nov.

Woods (1867b) figured *Hemipatagus forbesi* from either the Murray River or Mount Gambier, but many attributes depicted are inconsistent with the three *Lovenia* species described herein and so it cannot be identified. Laube (1869) also figured *L. forbesii* but this is considered inaccurate regarding characteristics of the sulcus and ambulacral columns.

Through discovery of the internal fasciole, Duncan (1877) transferred *H. Forbesi* to *Lovenia*, supplying four figures of specimens from the Murray cliffs, Mount Gambier, Mordialloc (Beaumaris) and the Hamilton Tertiaries (probably a Port Campbell Limestone equivalent). Three of the figures combine attributes of specimens derived from these different localities.

McCoy (1879) supplied four figures of *L. forbesi* (*sic*) based on specimens collected from similar localities as Duncan (1877) but with the addition of Torquay; figs 1 and 2 strongly resembling *L. woodsii*. Despite studying hundreds of specimens, McCoy reported that only one to three rows of primary tubercles develop in interambulacra 2a and 3b, yet four are common in all large specimens. The statement of two to five rows on the anterior part of the postero-lateral interambulacra suggests that the tubercles remain in the anterior half of the test, unlike *L. forbesii*.

In light of these inconsistencies, those descriptions by Duncan (1864, 1877) and McCoy (1879) are regarded inaccurate.

Species differentiation. The presence of primary tubercles in interambulacral columns 1a and 4b, a heart-shaped test, dorso-ventrally elongated periproct (Fig. 3) and anterior petals extending only half way to ambitus are unique to *L. forbesii*.

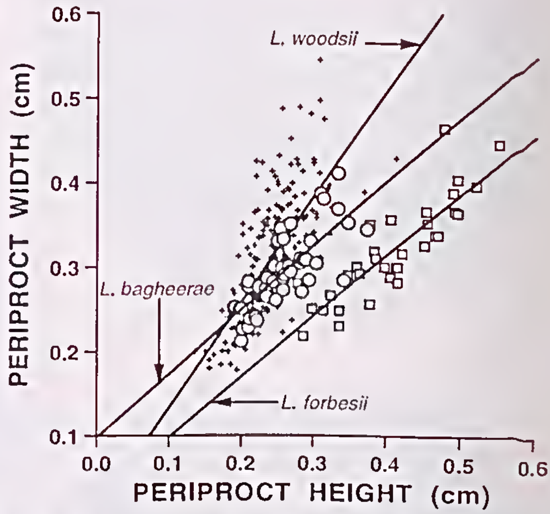


Fig. 3. Bivariate plot of periproct height vs. periproct width indicating intermediate nature of *L. bagheerae* sp. nov. (○) periproct as compared to horizontally and vertically elongate periprocts of *L. woodsii* (+) and *L. forbesii* (□) respectively.

Description. Test reaches a maximum known length of 50 mm; widest slightly anterior to mid-test length, resulting in heart shaped test. Width varies between 87–96% TL. Anterior test margin rises abruptly to internal fasciole, levelling out toward apical system, keel elevated immediately posterior to apical system, declining thereafter to posterior margin. Maximum height generally immediately posterior of apical system, however larger specimens have swollen ambulacrum III producing greatest height anterior of apical system. Height varies between 45–56% TL. Test has broad shallow anterior sulcus.

Apical system tetrabasal; tilted anteriorly, located about 40% TL of anterior; ethmolytic with four genital pores, smaller anterior pair closer than posterior; asymmetry of genital pores, left pair larger than right; madreporite oblanceolate, extending just posterior of ocular plates I, V; ocular pores very minute.

Adapically, ambulacrum III sunken, progressively deepening adorally, attenuating adapically, forming sulcus with peripheral coarse miliary tubercles of interambulacra 2b, 3a; ambulacrum bears minute adradial conjugate pores, size increasing adorally; more adoral pore displaced slightly perradial of adapical pore; pore pairs become more widely spaced adorally.

Antero-lateral ambulacral petals broad adapically, contracting abapically, terminating just over half-way to ambitus; anterior row of large pore pairs ½–⅔ length of posterior row; large pore pairs run almost transversely, smaller pore pairs subparallel to posterior row; angle of divergence of ambulacra IIb, IVa small pore pairs about 90°. Posterior row commonly straight, occassionally adapical half gently curved; terminates closer to apical system than anterior row; small pore pairs intersect apical system transversely; posterior rows diverge anteriorly at about 130°. Large pore pairs in petals conjugate, deeply recessed, anterior row reduced; adradial pore of each column more adoral, varying from similar in size to twice that of perradial pore; shape varies from orbicular to ovate with apex inclined adapically; pores closest to ambitus and apical system smallest; 9–13 pore pairs in column IIa, mean 11.2; 10–14 in IVb, mean 11.7; 4–9 in IIb, mean 6.5; 4–9 in IVa, mean 6.9; asymmetry with more pore pairs on left side of test.

Posterior ambulacral petals as wide as antero-lateral petals, terminate half-way to ambitus, both rows slightly sinuous, equal in length, divided anteriorly, merging posteriorly; angle of divergence of rows about 60°; ambulacra Ib, Va small pore pairs meet almost transversely. Large pore pairs commonly smaller or conjugates closer than in antero-lateral petals; 11–16 pore pairs in column Ia, mean 12.7; 11–15 in Vb, mean 13.2; 10–14 in Ib, mean 12.1; 10–15 in Va, mean 12.4; anterior rows shorter than posterior rows; asymmetry with more pore pairs on left side of test. Two aberrant specimens (NMV P78940, P78947) possess three pores in some plates of ambulacra I and V; extra pore small, orbicular, central between conjugate pores, displaced abapically.

Primary tubercles of adapical surface with perforate circular mamelon, flush with extrascrobicular surface, neck straight, platform impressed, surrounded by noncrenulate parapet; boss passes down imperceptibly into deep scrobicle; occassionally scrobicles coalesce near ambitus, rarely more adapically; tubercles absent from interambulacrum 5, occasionally occurring in 2b, 3a, more common in larger specimens; 0–1 primary tubercle in 2b, 3a, mean 0.2; échelon arrangement in 1b–2a and 3b–4a with tubercles sloping interradially downward, 1 to 4 rows per column; 3–13 primary tubercles in 1b, mean 7.8, 3–11 in 4a, mean 7.1; 3–13 in 2a, mean 8.0; 3–13 in 3b, mean 7.3; asymmetry with more primary tubercles on right side of test; tubercles present in anterior portion of 1a and 4b; 0–3 in 1a, mean 1.3; 0–3 in 4b, mean 1.4; asymmetry reversed compared to anterior half of test.

Primary tubercles of adoral surface confined to lateral margins; mamelon projects above extrascrobicular surface; scrobicle enlarged posterior of mamelon, boss confluent with anterior margin of scrobicle (Fig. 4C); tubercle size decreases adapically; tubercles of interambulacrum 5 restricted to dilated ends of spectacle-shaped fasciole (Fig. 4B), comparable in size to more ambital adoral tubercles, boss confluent with adapical margin of scrobicle; interambulacra 1, 4 tubercles occupy lateral region one-third of test width; tubercles of interambulacra 2, 3 restricted to ambital margin.

Entire apical surface granulated with close fine miliary tubercles; very minute granules comprise narrow internal fasciole (Fig. 4A); beginning just posterior of apical system perpendicular to posterior petals, forming obtuse angle, intersects antero-lateral ambulacra immediately above petal, then extends anteriorly with a slight inward convexity along outside of coarse miliary band bounding anterior sulcus, to a point about midway from apical system to ambitus. Periproct dorsoventrally oval (Fig. 3); longer axis 12–20% TL, shorter axis 9–15% TL; posterior margin slopes anteriorly from keel to adoral surface. Sub-anal fasciole large, spectacle shaped (Fig. 4B), lateral margins incorporate 4–6 small pore pairs of posterior ambulacra Ia, Vb.

Plastron smooth, posterior portion finely granulated as are adjacent episternal plates, producing radiating semicircle just anterior of sub-anal fasciole. Peristome overhung by anteriorly projecting labrum resulting in slight lunate shape; broad (Fig. 5), width being 14–19% TL with length between 6–11% TL; surrounded by phyllode. Base shape controlled by nature of interambulacrum 5; generally bulbous to arched.

Distribution. *L. forbesii* is very common in the Mannum Formation in the River Murray cliffs at Mannum, South Australia, and is considered by Ludbrook (1969) to be Longfordian (Burdigalian) in age. Sadler et al. (1983) indicated the uncommon occurrence of *L. forbesii* in the overlying Morgan Limestone of Batesfordian (Langhian) age, but this occurrence requires conformation.

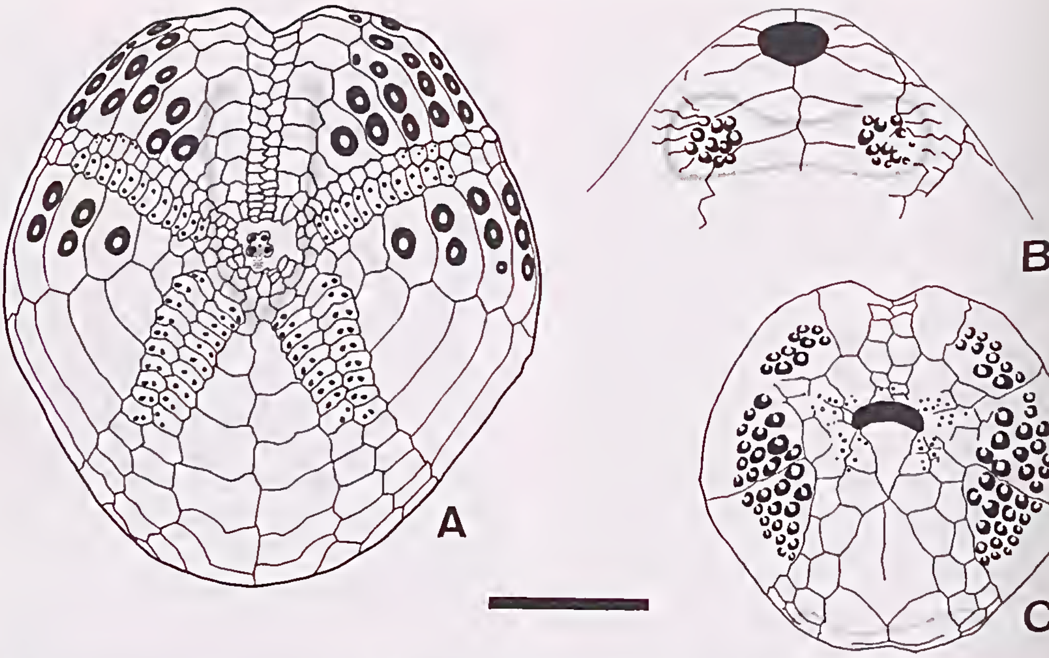


Fig. 4. *Lovenia woodsii* Etheridge. A, NMV P139210 adapical plating showing position of internal fasciole, pore pairs and distribution of primary tubercles. B, NMV P139210 posterior adoral surface indicating position of subanal fasciole. C, NMV P139211 adoral plating including phyllode. Scale bar represents 1 cm.

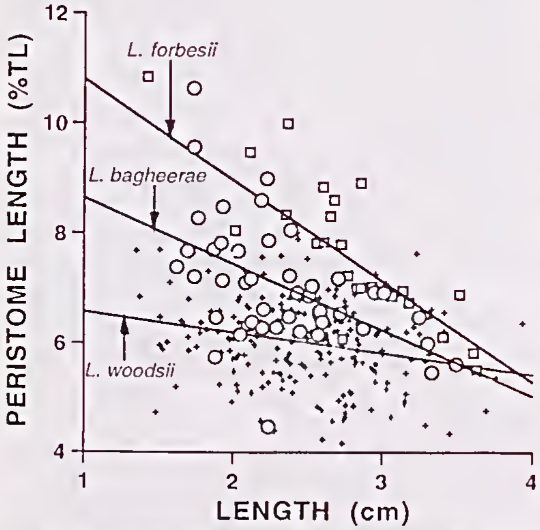


Fig. 5. Bivariate plot of peristome length expressed as a percentage of test length vs. test length indicating broad nature of *L. forbesii* (□) peristome compared to progressively narrower peristomes of *L. bagheerae* sp. nov. (○) and *L. woodsii* (+) respectively.

Lovenia woodsii (Etheridge 1875)

Figs 6, 7

Spatangus.—Forbes 1852: 50.
Spatangi.—Selwyn 1855: 5.
Hemipatagus Woodsii Etheridge 1875: 444–447, pl. 21, figs 1–7.—Woods 1878: 68.
Lovenia Forbesi, var. *minor* Duncan 1877: 44, 56–61, pl. 4, figs 5–8.—Etheridge 1878: 141.
Lovenia Forbesi, var. *Woodsi*, Etheridge.—Duncan 1877: 44, 56–61, pl. 4, figs 5–8.
Lovenia Forbesi, Woods & Duncan.—Duncan 1877: 44, 56–61, 63, pl. 4, figs 5–8.—Duncan 1887: 424–427.
Lovenia Forbesii, var. *Woodsii*, Etheridge.—Etheridge 1878: 141.
Lovenia Forbesii, Woods & Duncan.—Etheridge 1878: 141.
Lovenia Forbesi, McCoy.—McCoy 1879: 37–41, pl. 60, figs 1–4.
Lovenia Forbesi var. *Woodsii*, Etheridge.—Johnston 1887: 130.
Lovenia forbesi, Woods & Duncan.—Hall & Pritchard 1897: 191, 195.—Murray 1985: 190, pl. 7.9.23/A–C.
Lovenia forbesii, Woods & Duncan.—Hall & Pritchard 1897: 201, 202.
Lovenia forbesi, Woods.—Dennant & Kitson 1903: 132, 139.—Colliver 1937: 151, 153.—Singleton 1941: 33.—Kenley 1967: 38.

Lovenia woodsi, Etheridge.—Pritchard 1976 (1947): 20, fig. 11.—Philip 1957: 403.—Carter 1963: 166, pl. 27, fig. 9.—Philip 1963: 188.—Abele et al. 1976: 242.—Holmes 1987: 33, fig. 4.—Abele et al. 1988: 316.

Lovenia forbesi.—Carroll 1949: 105.—David 1950: 528, pl. 48e.—Rosengren 1988: 81, 83.

Lovenia forbesi var. *woodsi*, Etheridge.—Fletcher 1971: 134.

Lovenia.—Stone & Bawden 1975: 53, figured.

Lovenia woodsi.—Carter 1985: 17.—McNamara 1991b: 44.

Lovenia woodsii, Etheridge.—Archbold 1990: 119.

Lectotype. AM F17500, figured Etheridge (1875, pl. 21, figs 1–7) and Fig. 6 herein, from the Late Miocene Black Rock Sandstone, Beaumaris, on the east shore of Port Phillip Bay, Victoria.

Material and locality. NMV P139210–P139219 from the Cheltenhamian (Messinian) Black Rock Sandstone, Port Phillip Basin, from the cliffs behind and immediately west of Keefers Boatshed, 1.5 to 4 metres above sea level; NMV P139220, 218 specimens from the same locality as above (collected by N. W. Archbold).

Size ranges. Length 13.5–39.3 mm; width 13.1–37.3 mm; height 6.7–17.1 mm; width as % test length 88–103%; (mean 94%); height as % test length 38–56%; (mean 48%).

Diagnosis. Test diamond-shaped with maximum width half-way. Deep anterior sulcus. Primary tubercles few in number, restricted to anterior half of test; rare in interambulacra 2a/3b. Antero-lateral petals longer and narrower than posterior petals, terminate ⅔ of distance to ambitus, conjugate pore pairs diverge toward apical system, ambulacra IIb/IVa ¼–⅓ length of IIa/IVb. Periproct compressed in dorso-ventral plane, peristome antero-posteriorly narrow.

Description. Maximum test length of 40 mm; widest about mid-test length, producing diamond shaped test. Width varies between 88–103% TL. Height varies between 38–56% TL. Distinct anterior sulcus.

Apical system slightly anterior of mid-test length;

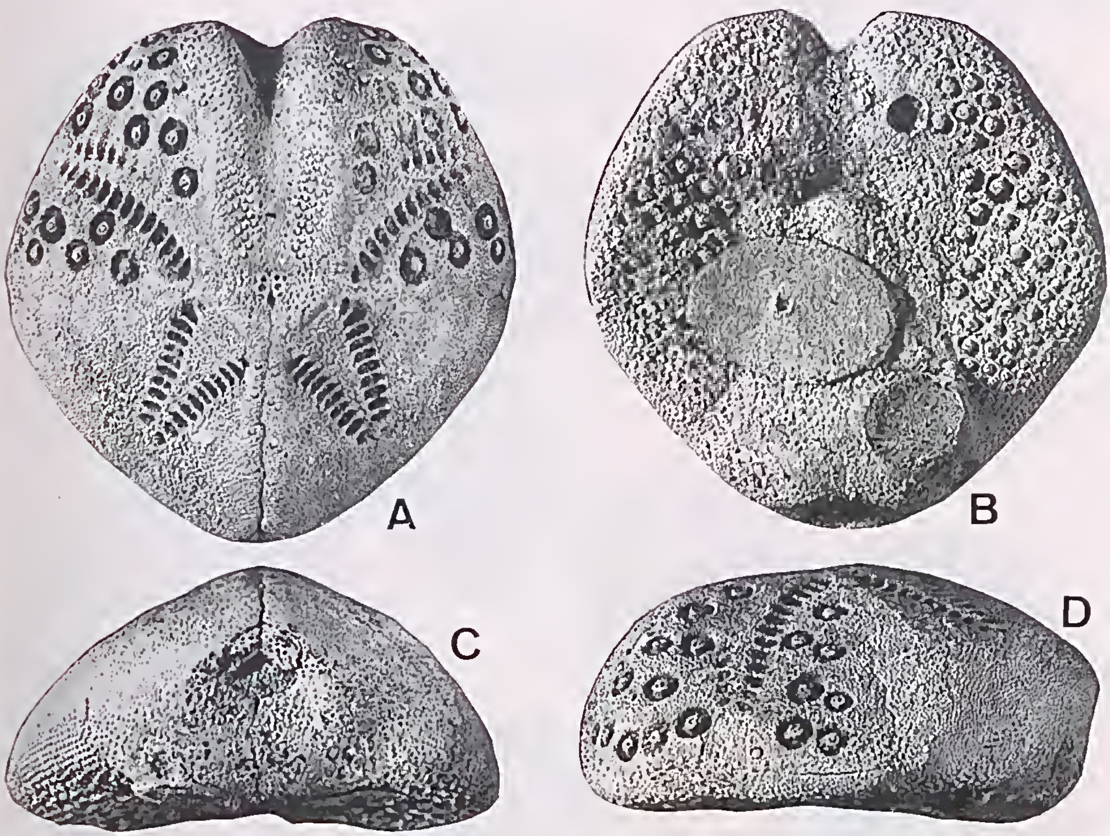
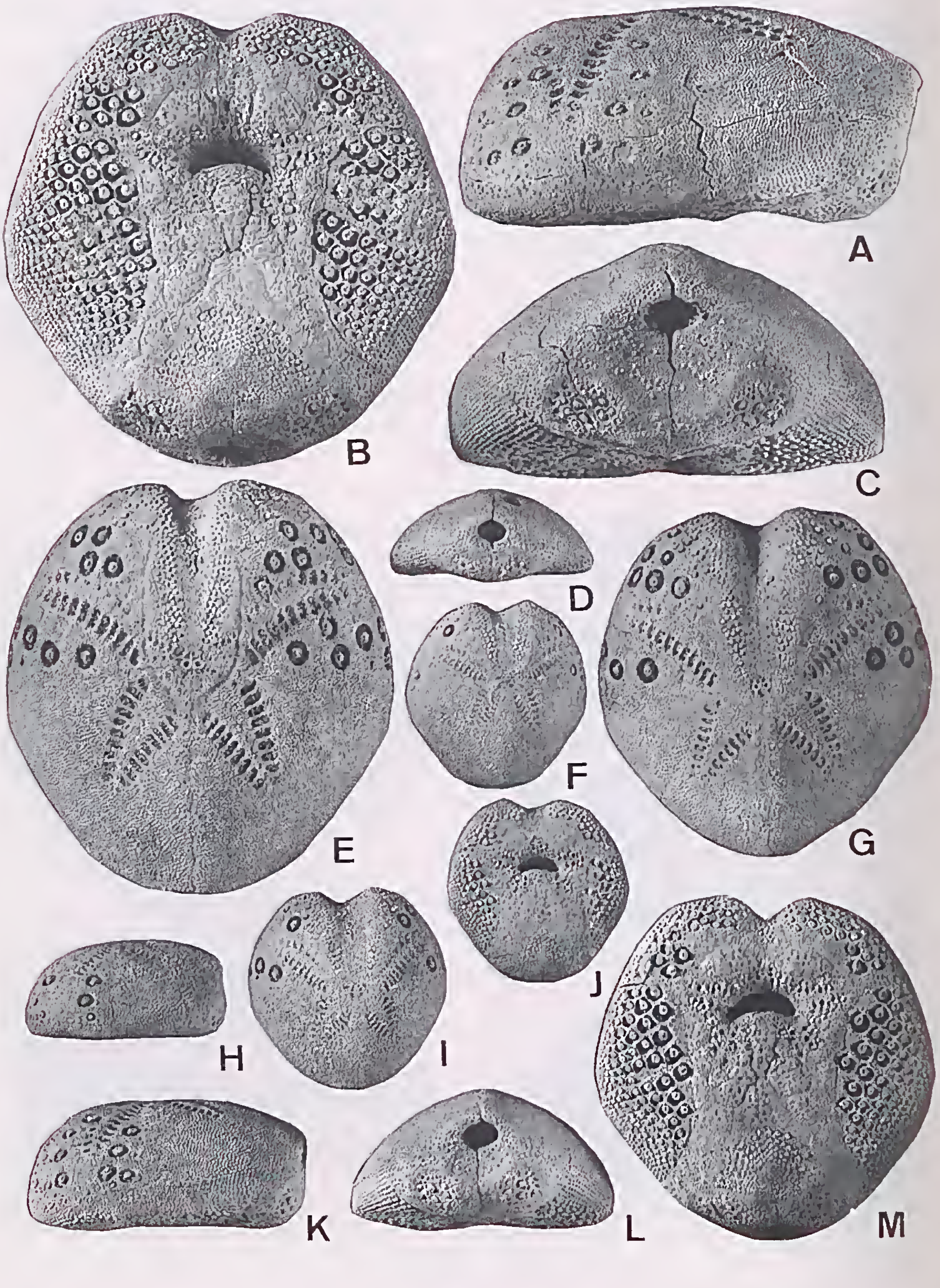


Fig. 6. A–D, *Lovenia woodsii* Etheridge. All figures ×2. A–D, AM F17500, holotype, adapical, adoral, posterior and lateral views.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madreporite obovate, greatly separating posterior genital pores. Antero-lateral ambulacral petals terminate two-thirds distance to ambitus; anterior row of large pore pairs varies from ⅓–¼ posterior row length; conjugate pore apices linked by adapical ridge forming oval pit adorally. Ambulacra IIb, IVa small pore pairs diverge at about 90°, posterior rows diverge anteriorly at about 110°. 8–12 pore pairs in column IIa, mean 10.13; 9–13 in IVb, mean 10.68; 1–6 in IIb, mean 3.66; 1–6 in IVa, mean 3.60.

Posterior ambulacral petals wider than antero-lateral petals (Fig. 4A), both rows straight, equal in length; angle of divergence of anterior row about 50°, posterior row about 90°. Large pore pairs similar in size to antero-lateral petals; 6–11 pore pairs in column Ia, mean 8.4; 7–12 in Vb, mean 8.8; 6–10 in Ib, mean 7.8; 6–11 in Va, mean 8.1.

Primary tubercles absent from interambulacral columns 1a, 4b and 5a, b, rarely present in 2b and 3a, larger specimens exhibiting infrequent development; 0–2 primary tubercles in 2b, 3a, mean 0.1; 1 to 4 rows in columns 2a, 3b, 1 to 3 in 1b–4a; 2–11 primary tubercles in lb, mean 4.9, 1–9 in 4a, mean 4.7; 2–14 in 2a, mean 6.6; 2–15 in 3b, mean 6.3. One aberrant specimen (NMV P139212) possessed one primary tubercle in interambulacrum 4b.

Periproct laterally elliptical (Fig. 3); longer axis 9–20% TL, shorter axis 7–14% TL; keel overhangs periproct producing concave posterior margin, termed beaked condition.

Peristome overhung by slightly bowed labrum, resulting in semi-circular to slight lunate shape (Fig. 4C); narrow (Fig. 5), length being 4–8% TL with width between 11–23% TL. Base shape generally flat to concave.

Remarks. This species has often been confused with *L. forbesii*, e.g. Singleton (1941), Kenley (1967) and Rosengren (1988). Hawkins (1916) reported on plate-crushing and resorption in the interambulacra of *L. forbesi* (*sic*) from no indicated locality, but as previously indicated by Philip (1957), the dimensions provided for the two specimens, 546A and 546B (housed in the University College, Reading, U.K.), suggest *L. woodsii*, as does Davies' (1935) figured *L. forbesi* (*sic*) from Victoria. However, accurate identification requires direct examination of the material.

Etheridge (1875) supplied four figures which closely approximated the species, but exaggerated the number of pore pairs. Aslin (1980) reproduced those illustrations but further exaggerated those attributes which were erronous in the originals. Carter's (1963) topotype is a further example of an inaccurate illustration with pronounced asymmetry of the pore pairs, most of which exceed the observed range.

Pritchard (1976) provided an accurate series of diagrams in his fig. 11 of *L. woodsii*, as did Holmes (1987), fig. 4, with the exception of an abnormally high number of pore pairs in columns IIb and IVa.

Species differentiation. *L. woodsii* differs from *L. bagheerae* in its lower comparative number of adapical primary tubercles (Fig. 8), adapical divergence of the antero-lateral conjugate pore pairs and laterally elongated periproct (Fig. 3). Obvious in comparisons between populations is the antero-posteriorly narrow peristome (Fig. 5) and lesser number of pore pairs, apparent in ambulacra IIb (Fig. 9) of *L. woodsii*.

Distribution. *L. woodsii* is common at Beaumaris, being restricted to the Cheltenhamian (Messinian) Black Rock Sandstone of the Brighton

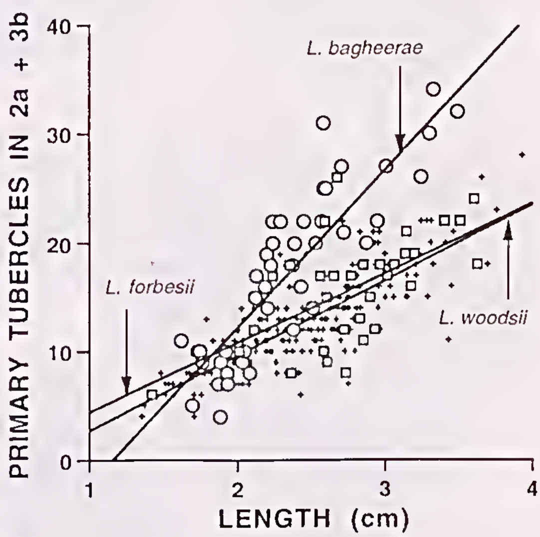


Fig. 8. Bivariate plot of combined number of primary tubercles in interambulacral columns 2a, 3b vs. test length showing increased attainment in *L. bagheerae* sp. nov. (○) as compared to *L. woodsii* (+) and *L. forbesii* (□).

Fig. 7. A–M, *Lovenia woodsii* Etheridge. All figures ×2. A–C, NMV P139213, lateral, adoral and posterior views; D, NMV P139218, posterior view; E, NMV P139214, adapical view, note internal fasciole; F, J, NMV P139219, adapical and adoral views; G, M, NMV P139215, adapical, and adoral views; H, I, NMV P139217, lateral and adapical views; K, L, NMV P139216, lateral and posterior views.

Group. Johnston (1877, 1888a, 1888b) reported *L. woodsii* from Table Cape, Tasmania, but it is likely that the speeies is either *L. forbesii* or an as yet undeseribed phenotype.

Sadler et al. (1983) reeorded *L. woodsii* from both the Morgan Limetone and Loxton Sands. If so the range of *L. woodsii* would span the Mioeene and inelude the Plioeene as far as the Kalimnan (Zanelean).

Lovenia bagheerae Irwin sp. nov.

Fig. 10

Spatangus Forbesii.—Woods 1859: 91.—Woods 1862: 121.
Hemipatagus Forbesi, Woods & Duncan.—Woods 1865: 12.
Hemipatagus Forbesii, Woods & Duncan.—Woods 1865: 17, 19.
Lovenia Forbesii, Woods & Duncan.—Etheridge 1878: 141.—Woods 1878: 74.
Lovenia Forbesi, McCoy.—McCoy 1879: 37–40, pl. 60, figs 1–4.
Hemipatagus forbesii.-Dennant 1890: 445.
Lovenia forbesi, Woods.—Dennant & Mulder 1898: 86.—Dennant & Kitson 1903: 132.
Lovenia woodsi, Woods.—Chapman 1916: 401.
Lovenia woodsi, Etheridge.—Carter 1963: 166, pl. 27, figs 1, 2.—Abele et al. 1976: 214.—Abele et al. 1988: 288.
Lovenia woodsi.—Singleton 1968: 127.—Singleton 1973: 124.
Lovenia.—Mallett 1977: 79.

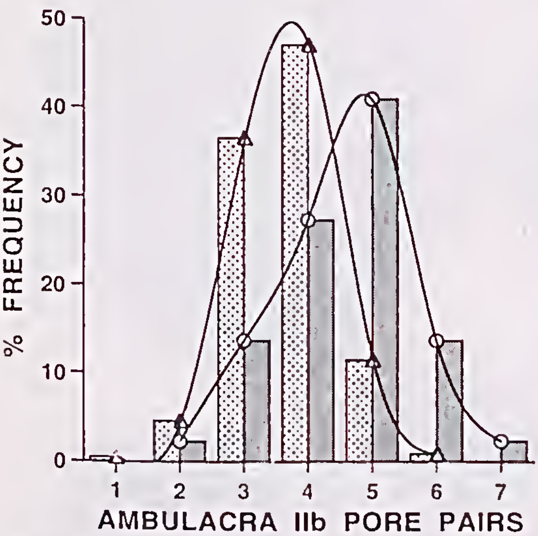


Fig. 9. Histogram of frequency of total number of pore pairs in ambulacral column IIb for *L. woodsii* (△) and *L. bagheerae* sp. nov. (○) depicting similarly shaped but juxtaposed bell curves.

Etymology. Bagheera: P. Irwin's pet black cat (female), in loving memory of a very close friend.

Holotype. NMV P79247 from the early Late Mioeene Mitchellian (Tortonian) Port Campbell Limestone, Portland, 300 km west of Melbourne, Victoria; F. A. Cudmore collection.

Paratypes. NMV P79233–P79270 ineluding P78918, P78927, P78935, P78941, P78943 and P78953 from the same member/horizon and locality as the holotype.

Size ranges. Length 16.2–34.9 mm; width 5.9–32.6 mm; height 8.6–17.6 mm; width as % test length 88–99%; (mean 94%); Height as % test length 46–56%; (mean 51%).

Diagnosis. Test diamond-shaped with maximum width half-way. Deep anterior suleus. High density of primary tubereles eonfined to anterior half of test; common in interambulaera 2a/3b. Antero-lateral petals longer and narrower than posterior petals, terminate ⅔ of distanee to ambitus, eonjugate pore pairs do not diverge toward apieal system, ambulaera IIb/IVa ⅓ length of IIa/IVb. Periproct almost eircular, peristome antero-posteriorly broad.

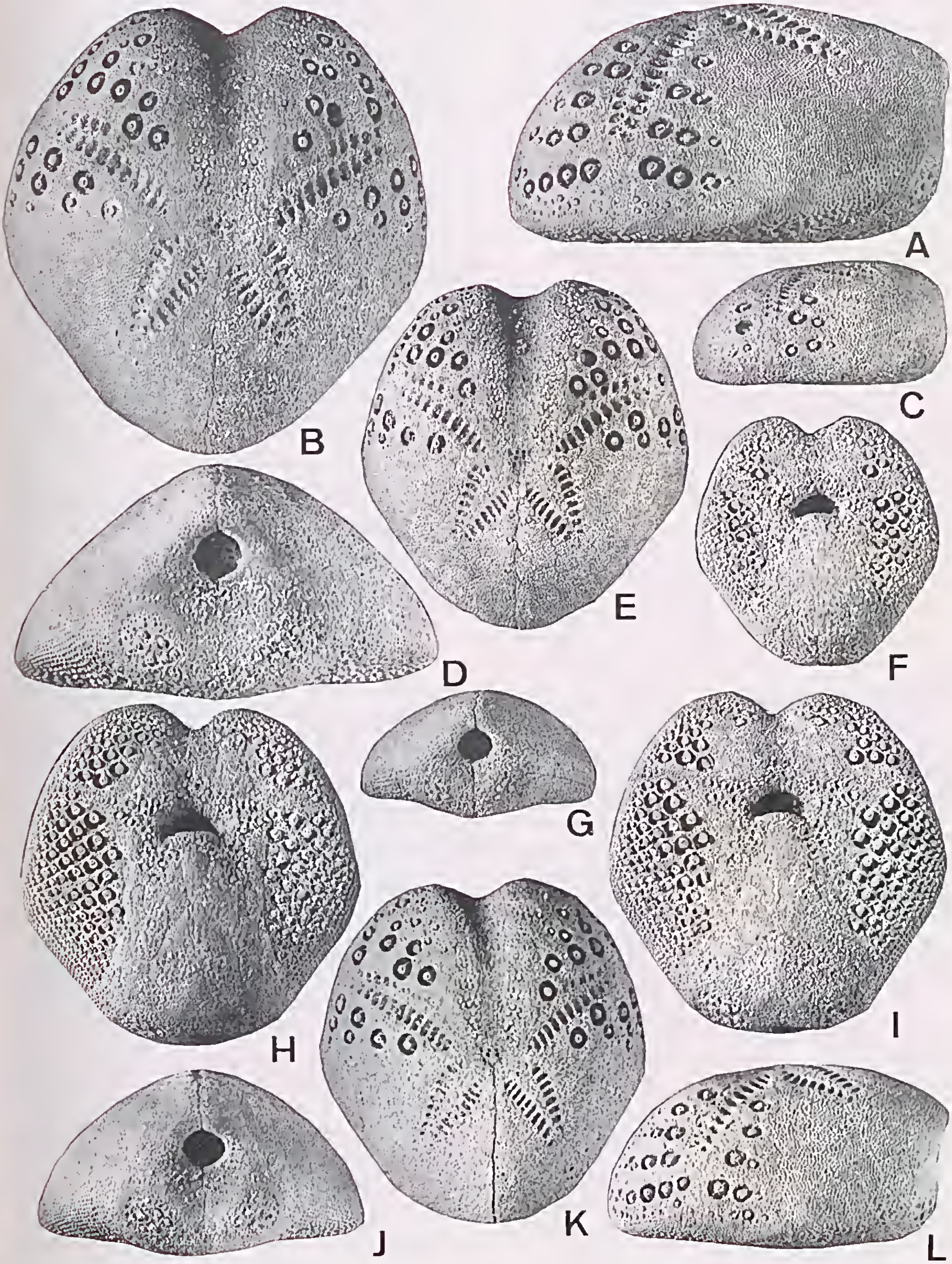
Description. Test reaehes a maximum known length of 35 mm; widest slightly posterior to mid-test length, produeing diamond shaped test. Width varies between 88–99% TL. Height varies between 46–56% TL. Anterior suleus pronouneed. Apical system slightly posterior of mid-test length.

Posterior rows of antero-lateral petals diverge anteriorly at about 120°; anterior rows parallel posterior rows, barely diverging adapieally; 9–14 pore pairs in eolumn IIa, mean 10.4; 8–14 in IVb, mean 11.2; 3–7 in IIb, mean 4.6; 2–7 in IVa, mean 4.5.

Divergenee of anterior row of posterior ambulaera about 45°, posterior row about 60°. 8–12 pore pairs in eolumn Ia, mean 9.4; 8–12 in Vb, mean 9.6; 7–12 in Ib, mean 8.8; 7–11 in Va, mean 9.1.

Primary tubereles in 2b, 3a eommon for large speeimens (Fig. 8), less frequent at smaller size;

Fig. 10. A–L, *Lovenia bagheerae* sp. nov. All figures ×2. A, B, D, NMV P79263, paratype, lateral, adapical and posterior views; C, F, G, NMV P79254, paratype, lateral, adoral and posterior views; E, H, J, L, NMV P79247, holotype, adapical, adoral, posterior and lateral views; I, K, NMV P79248, paratype, adoral and adapical views.


A
B
C
D
E
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L

0–2 primary tubercles in 2b and 3a, mean 0.4; 1 to 5 rows in columns 2a–3b, 1 to 4 in 1b–4a; 1–11 primary tubercles in 1b, mean 5.9, 1–10 in 4a, mean 5.6; 1–18 in 2a, mean 9.0; 2–16 in 3b, mean 8.1. Three aberrant specimens (NMV P79242, P79254, P79262) possessed one primary tubercle in interambulacrum 1a or 4b.

Periproct obovate to rhomboidal (Fig. 3); laterally 8–18% TL, dorso-ventrally 10–17% TL. Sub-anal fasciole incorporates 3–5 small pore pairs of ambulacra Ia, Vb.

Peristome length 4–11% TL, width 12–20% TL. Base shape generally bulbous to arched.

Remarks. Woods (1859) was the first to observe this species, classifying it with the Mount Gambier taxon as *Spatangus Forbesii*. Duncan's fig. 3 (1864), based on specimens from the Murray or Mount Gambier was likewise considered to represent a *L. forbesii* but is most representative of *L. bagheerae* sp. nov. despite an exaggerated number of pore pairs in the anterior rows of the anterior petals. Etheridge (1878), McCoy (1879), Dennant (1890), Dennant & Mulder (1898) and Dennant & Kitson (1903) all assimilated the Portland population into *L. forbesii*.

Chapman (1916), Singleton (1968, 1973) and Abele et al. (1988) considered the population at Portland to be *L. woodsi* (*sic*), as did Carter (1963), figuring what could loosely be considered *L. bagheerae* sp. nov. Mallett (1977) classified the population to genus only.

McNamara (1987, 1989, 1990, 1991a) and Holmes (1987) alluded to three Tertiary species of *Lovenia* from south-east Australia, McNamara (1991a) indicating the Peterborough Member of the Port Campbell Limestone, this upper Middle Miocene Member being found only in the Port Campbell Embayment (Abele et al. 1988), Holmes indicating an Early Pliocene age for a friable limestone from Portland. The reported ages of Middle Miocene and Early Pliocene for the unnamed species do not conform with the Late Miocene Mitchellian (Tortonian) stage assigned to that part of the Port Campbell Limestone which is found to outcrop in the Portland cliffs (Singleton et al. 1976) from which *L. bagheerae* sp. nov. is derived.

Distribution. This new species has been described solely from material collected from Portland, Victoria. The specimens were removed from that section of the Port Campbell Limestone representing the upper part of zone N16 and the basal part of zone N17 (Singleton et al. 1976, Abele et al. 1988), making *L. bagheerae* sp. nov. Mitchellian (Tortonian) in age.

If Duncan's fig. 3 (1864) of *L. woodsii* (*sic*), reportedly from either the Murray River or Mount Gambier is *L. bagheerae* sp. nov. then the time range would extend to the Late Oligocene. Verification of temporal and spatial distributions is required to resolve which species are present as preliminary evidence points toward a larger number of species than is currently known.

ONTOGENY

Investigation of the post-juvenile ontogenetic series revealed considerable change in terms of size, shape and number of the morphological features. Most attributes exhibit allometric growth during development with the resultant ontogenetic changes being: a relative decrease in both the lateral and dorsoventral size of the periproct compared to the test length; a relative decrease in the lateral and anteroposterior (Fig. 5) size of the peristome relative to the test length; a progressive increase in the defensive adapical primary tubercles (Fig. 8) and the lateral burrowing adoral primary tubercles; an almost negligible increase in the number of petaliferous pore pairs; a slight reduction in the height and width of the test compared to test length, except for *L. forbesii* which shows a minor increase in both.

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